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# Maine Agricultural Experiment Station

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## NORMAL AND ABNORMAL GERMINATION OF GRASS-FRUITS.

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BULLETIN 294

NORMAL AND ABNORMAL GERMINATION OF  
GRASS—FRUITS.\*

BY

JACOB ZINN.

SUMMARY

The present paper is an account of the processes that take place at the time of emergence of the radicle of hulled grass-fruits from the surrounding tissues.

The penetration of the germinating embryo through the tissues of the adhering pericarp is a purely mechanical process. Under the pressure of the extending embryo a section of the tissues yields at a certain point and usually in a certain direction.

At normal germination the coleorhiza breaks through the base of the fertile glume within a zone whose mechanical resistance is greatly lessened by the marked reduction and differentiation of the epidermal and hypodermal mechanical cells. The prosenchymatous tissue yields along lines of contact of the long sclerenchymatous cells and the short basal elements of the glume. Likewise, the epidermis is ruptured in a region where cells marked by different morphological forms and physical structure meet. In both cases the cells are pushed apart, the sclerenchymatous cells remaining, as a rule, intact while the epidermal cells mostly escape injury. The tracheal elements of the fibro-vascular bundles have been invariably found to be broken through.

The abnormal germination of hulled grass-fruits is caused by external mechanical factors prevailing in artificial germination media which operate so as to thwart and eliminate the

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\*This is an abstract from a paper by the author having the title: "Ein Beitrag zur Keimungsgeschichte der bespelzten Grassfrüchte," and published in "Mitteilungen der landw. Lehrkanzeln der k. k. Hochschule für Bodenkultur," Vol. II, pp. 675-712, 8 pl. 24 figs. Wien, 1914.

growth tendency of the radicle in the normal direction. As a result of this interaction between normal growth-tendency and growth-inhibition the radicle takes its way in the direction of least resistance.

At germination in natural media in the soil, the factors obtaining in artificial germinators are not present and accordingly the abnormal germination is either entirely absent or occurs only to a very limited degree with some grasses.

Likewise, the second consequence of the operation of conditions prevailing in the germinator, i. e. the dying off of the radicle within the glumes, either does not occur at all or only very rarely at germination in the soil.

The rupture of the tissues of the glumes is effected, as a rule, by the coleorhiza. It accomplishes this chiefly by means of its turgescence and may be assisted in this work by the short and thick cells of its apical tissues.

The chief function of the coleorhiza is its mechanical performance in breaking through the tissues of the glume, it further functions as a protective organ for the tender radicle and cares by means of its hairs or trichomes for the fastening of the seedling to the soil particles, thus assisting the radicle in its penetration into the soil.

The occurrence of the trichomes as observed in the course of the investigation in a large number of grasses justifies the conclusion that the formation of hairs is a general characteristic of the coleorhiza of the Gramineae.

The radicle emerges from the coleorhiza of grass-fruits through a longitudinal, lateral opening formed by the cells being detached and pushed apart without being injured in any way.

#### INTRODUCTION.

The anatomical and mechanical processes accompanying the passage of the germinating embryo through the glumes of the grass-fruits, especially of the true grasses, have hitherto been given but little attention. Although the germination of the Gramineae has long been studied with great interest, the chief attention was centered on the cereals while the true grasses were generally subordinated to them.



The presence of flowering glumes and—in certain species—sterile glumes enclosing the caryopsis, the development of long and thick trichomes on the coleorhiza of grass-fruits as compared with the short and scant hairs on the coleorhiza of cereals, the sending out, at the beginning of germination, of the main radicle alone instead of several rootlets as in the case of the germinating caryopsis of cereals, and finally the various types of abnormal germination reported in this paper, are all features peculiar to the true grasses and interesting enough to warrant a separate consideration of the germination of grass-fruits.

The present account is an attempt to follow the germinating embryo of the hulled grass-fruits on its way through the surrounding tissues, and to record the anatomical changes and mechanical processes accompanying germination.

The changes in the anatomy of the pericarp caused by the germinating embryo have not been examined in this study.

The material for this investigation comprises chiefly the economically important grasses. In the course of this study over 18,000 seedlings were examined. The illustrations, some of them hand drawings from nature, were all made by the writer.

## I. NORMAL GERMINATION OF GRASS-FRUIITS.

### I. THE PENETRATION OF THE COLEORHIZA THROUGH THE PERICARP.

The first stages of the process of germination of the hulled grass-fruits take place in a manner similar to the general type of the Gramineae. Germination begins with the absorption of water. The germ becomes turgescient and lies now close to the pericarp. Contrary to the germination of the Cyperaceae and some other monocotyledonous plants the first symptoms of growth are normally visible at the base of the embryo. First the coleorhiza extends and strikes upon the pericarp. No record is available of the anatomical changes in the pericarpial tissues caused by the breaking through of the coleorhiza. Nor are the macroscopic descriptions of this stage in the germination concordant.

The few references to be found in the literature do not indicate which part of the embryo breaks through the pericarp. If the embryonic region of a naked caryopsis of *Alopecurus* or *Arrhenatherum* be examined with a low power lens at the first stage of germination, it will be noticed that under the pressure of the extending coleorhiza a small aperture is formed above the hilum in which the tip of the coleorhiza appears. This aperture soon gives rise to a slit which tends upwards, usually in the middle plane of the embryo, and grows wider being extended by the growing coleoptile up to the inner edge of the scutellum. On removing the germinating embryo from the caryopsis a more or less elliptical opening will be seen with the separated edges of the pericarp projecting over it. Thus the rupture of the pericarp takes place usually in a definite direction and, as a rule, is effected by the extending coleorhiza. During this process no loss of tissues occurs. This is worthy of being mentioned since one might be inclined to assume in connection with this process the operation of chemical agencies that would loosen and absorb the tissue elements.

## 2. THE PENETRATION OF THE COLEORHIZA THROUGH THE LEMMA.

After breaking through the tissues of the pericarp the coleorhiza encounters the basal wall of the fertile glume or lemma. The basal region of the lemma presents a detail of special importance in connection with the breaking through of the coleorhiza. At its base the lemma of the grass-fruits forms a semi-globular, disk-like or obtuse-conical callus which is separated from the main body of the lemma by a transverse furrow, and which is connected with the rachilla by means of a joint. In this region a marked differentiation of tissues occurs. Before describing the anatomical details of this region it is advisable first to briefly discuss the tissue elements of the lemma.

The lemma is composed of the outer and inner epidermis and of the mesophyll enclosed by them. The elements of the outer epidermis which forms the most powerful part of the lemma in most grasses, are distinguished by their wavy longitudinal walls whose indentations are most pronounced in the middle section of the lemma. Here, as will be seen in Fig. 33



the wavy lines of the longitudinal cell-walls are transformed into transverse processes, which with some grasses attain a length equaling the width of the cell. These transverse processes of the longitudinal walls fit into the corresponding indentations of the adjoining cells thus establishing a mechanical resistance of this system of tissues in the longitudinal direction. Embedded in between the longitudinal walls of the adjoining cells are thick silicious cells, one-celled and two-celled little hairs. These function as rivets, so to speak, establishing a connection of the cells in the longitudinal direction and preventing a dislodging of the epidermal cells in the transverse direction. The mechanical firmness of this system of tissues is further enhanced by the thickening and silicifying of the cells. The mesophyll beneath the epidermis is differentiated into two layers: The prosenchyma composed of specific mechanical cells and the parenchyma made up by thin-walled cells carrying chlorophyll at their early stage of growth. The prosenchyma is composed of elongated, very thick, porous, spindle-shaped cells, (Fig. 35, C.) which owing to their very marked growth in the longitudinal direction, interlock with each other. (Fig. 35, A.). The lemma of the true grasses contains usually 1-3 layers of these cells. The number of layers of parenchymatous cells increases towards the vascular bundles. As will be seen later this increase in parenchymatous tissue around the vascular bundles and at the base of the lemma is of importance in connection with the breaking through of the coleorrhiza. Beyond the marginal vascular bundles the cells of the parenchyma become thick-walled, their lumen decreases as well as their number until at the edge of the lemma they disappear. The sclerenchymatous cells undergo a similar reduction so that at the lower outer edge of the lemma the thick-walled cells of both the outer and inner epidermis lie upon each other.

The inner epidermis is composed of thin-walled, elongated, colorless cells, possessing, when young, a very large lumen.

The differences in thickness and tenacity of the lemmas of different grasses is caused by the variation in the number of cell layers and the degree of thickening of the elements of the outer epidermis and the prosenchyma.

Returning now to the processes occurring during the first stages of germination, the coleorrhiza, after breaking through the pericarp, directs the energy of its turgescent cells against the

mechanical resistance of the basal zone of the lemma. The turgor increases with the growing activity of the coleorhiza and reaches a point when it equals the resistance of the lemma. If the coleorhiza is now to effect the breaking through the lemma it is essential that the caryopsis be properly anchored so as to avoid its being pushed back or aside by the presence of the extending coleorhiza. Normally, the caryopsis at germination in artificial media is prevented from receding by its firm cohesion to the palet, and occasionally, to the lemma. The pressure of the coleorhiza exerted against the base of the lemma finally overcomes the resistance of the latter and a rupture of the tissue in that region ensues.

The macroscopic aspect of the rupture at the base of the lemma varies somewhat with different grasses but with the same species it always occurs in a definite manner. On examining the germinating caryopsis of *Lolium italicum* or *Festuca arundinacea* just previous to the appearance of the tip of the coleorhiza, it will be noticed that the primary fissure runs in a transverse direction, generally along the basal furrow above the callus referred to above. Soon after, the pressure of the protruding coleorhiza causes the tissues at the base of the lemma to split forming longitudinal slits which extend upwards for some distance. The section of the lemma, severed from its base by the coleorhiza, may either be bent off as a coherent piece (*Lolium italicum*, *Festuca arundinacea*, *Panicum miliaceum*) or split into more or less wide stripes (*Arrhenatherum*, *Dactylis*, *Avena*, *Holcus*). The primary transverse fissure was never found to extend beyond the marginal vascular bundle.

While these conditions are typical of the majority of hulled grass-fruits, the coleorhiza of certain grasses breaks through the lemma in a manner somewhat different from the one just described, and characterized by the longitudinal slit occurring in a distinct region and direction. To this group belong grasses whose caryopsis and glumes are flattened, the embryo facing the strongly carinated, dorsal, fibrovascular bundle of the lemma, e. g. *Alopecurus pratensis*, *A. geniculatus* and *A. agrestis*, *Phalaris arundinacea* and *canariensis*, *Oryza sativa* and *Bromus Schraderi*. Here the rupture of the lemma occurs along a line of contact of the parenchyma and the median fibrovascular bundle. With the exception of a few cases—in the glume of



*Alopecurus pratensis*, and *A. agrestis*, and the lemma of *Oryza sativa*,—the writer has not observed a splitting of the fibrovascular bundle, at germination. The separation of the fibrovascular bundle from the parenchyma may be observed very distinctly in *Phalaris arundinacea* and *Phalaris canariensis*. Here two types of cleavage may occur. The coleorhiza may, like in *Alopecurus*, either cause a slit which is continued along the fibrovascular bundle, or, the median fibrovascular bundle may be ruptured at the base of the lemma and separated from the latter by two parallel longitudinal slits running along its sides. With *Alopecurus* the tissue at the base is not ruptured at germination probably on account of the flattened, spatula-like shape of the coleorhiza whose pressure is directed against only a narrow zone, in the plane of the median vascular bundle.

The penetration of the coleorhiza through the powerful obstacle presented by the lemma would require such a considerable effort that one must assume the presence of certain arrangements in the structure of the lemma, tending to reduce its resistance and facilitate the task of the coleorhiza. An investigation into the tissues of the lemma revealed a very marked differentiation and reduction of the tissues in the basal region of the lemma.

Considering first the tissues of the lemma of *Lolium italicum*, it will be seen that the epidermis, throughout the greater part of the lemma is built with a view to mechanical firmness (Fig. 33.). Towards the base, however, the jagged processes of the longitudinal walls of the epidermal cells decrease and ultimately disappear, the walls assuming a wavy aspect. The silicious cells likewise disappear so that here the contiguous epidermal cells touch each other directly with their septæ. In the proximity of the base of the lemma the epidermal cells become thin-walled, their longitudinal and transverse diameter decrease and finally they assume the aspect illustrated in Fig. 34 (upper part). A comparison of Fig. 33 with Fig. 34 will afford sufficient evidence of the changes in the epidermal cells. After forming the transverse basal groove the epidermal cells enter the basal callus.

The callus presents a very interesting anatomical detail. With *Lolium italicum* it has a flat semi-globular form, and over its upper edge extend the above-named super-basal cells of the



epidermis which at this point assume an irregular and peculiar shape (Fig. 34, lower part). They appear here short and broad, and have a more transverse orientation, which is of importance in connection with the breaking through of the coleorhiza. Following these cells is a layer of strongly thickened, silicious, mainly hexagonal cells. They lie parallel to each other and are, about the middle of the base, arranged in longitudinal series while at either side of the base they form transverse, fan-like layers. These cells terminate with a ring of quite short, roundish-polygonal cells which form the outermost lower border of the base of the lemma. With this ring of short cells the lemma rests upon the rachilla. The rachilla appears as a columnar pillar whose elements are composed of elongated cells. The epidermal cells are very thick, appear round on cross-section, and some of them run out into hairs. The epidermis is followed by 2 to 3 layers of thick-walled, pitted, sclerenchymatous cells while the parenchymatous tissue fills out the central part of the rachilla, and surrounds the fibrovascular bundles. Towards the base of the lemma the rachilla broadens somewhat and its long cells terminate with a ring of quite short round cells which border directly on the ring of similarly developed cells forming the lowermost layer of the base of the lemma. At maturity these two rings separate and the fruit thus becomes detached from the rachilla.

No less striking is the differentiation of the mechanical elements of the prosenchymatous tissue. As will be seen from Fig. 35 A. a. C. this tissue is composed above the basal region of the lemma of elongated, interlocking, pointed sclerenchymatous cells. At the base, however, they lose their sclerenchymatous aspect, their longitudinal diameter decreases, their lumen increases, their pointed ends are transformed into oblique or almost horizontal septae until they assume an entirely different aspect at the base of the lemma, as illustrated in Fig. 35 B.

This differentiation in form is accompanied by a reduction in the number of presenchymatous cell-layers in the region where the coleorhiza breaks through. While above the base the prosenchyma is composed of 5-7 layers, it is reduced at the base to but one layer. The reduction of the epidermis is also caused by the disappearance of silicious cells and the decrease in the thickness of the cell walls. However, along the outer edge of the

marginal fibrovascular bundles in the lower region of the lemma, the prosenchyma forms a strong layer of mechanical cells, which enter the base and penetrate it transversely. A part of them resolve themselves about the middle of the base into short cells, while most of them connect with the tissues of the rachilla bearing the upper spikelet. This rachilla has a pillar-like form composed of long, pitted, cells which terminate at the apex with a ring of short cells upon which the base of the upper spikelet rests. Towards its lower end the rachilla broadens and enters the base of the lemma of the lower spikelet. Its central tissue runs out into small cells while the lateral cell layers on entering the base of the lemma of the lower spikelet turn outwards, become short-celled, and join the lateral layers of the base referred to above. The point of juncture of these two cords of tissues affords a very interesting mechanical detail. Here peculiar knee-shaped cells are found which penetrate with their pointed ends into the intercellular spaces of the two tissue-cords thus establishing a joint between the base of the lemma of the lower and the rachilla of the upper spikelet. This hinge-like detail enables the lemma to execute a turning movement at the time of bloom.

To complete the description of the base of the lemma it may be added that here we find the point of junction of the fibrovascular bundles. The three fibrovascular cords on entering the base branch out, five bundles entering the lemma while the remainder goes off to the upper rachilla and palea.

The changes in the epidermis and prosenchyma occurring at the base of the lemma can also be studied on transverse sections. (See Figs. 36, 37, 38). Fig. 36 represents a section below the point at which the coleorhiza breaks through, showing the thick-walled, pitted cells of the outer epidermis and the likewise thick-walled cells of the prosenchyma. Fig. 37, illustrates a cross-section of the base of *Festuca arundinacea*, about the line of rupture. Here a remarkable differentiation in the direction of the transverse axis can be noticed. The cells of the prosenchyma to the right of the lateral fibrovascular bundle, towards the median bundle, become thick-walled and finally assume a sclerenchymatous aspect while towards the marginal nerve they possess thin walls and differ little from the parenchymatous tissue. The latter decreases towards the median bundle and finally becomes reduced to 2 layers. From the lateral fibrovascular bundle to the marginal the paren-

chyma gradually increases, attaining its greatest extension near the marginal bundle. Thus the parenchyma predominates in the region between the lateral and marginal vascular bundles and as a result the tissue of the lemma of *Festuca arundinacea* and other grasses is ruptured by the coleorhiza between these two fibrovascular bundles.

The very remarkable aspect which the tissues of the lemma assume above the line of rupture is illustrated in Fig. 38 which represents a section between the lateral and marginal fibrovascular bundles, corresponding to the one given in Fig. 37 (around the median bundle.) A comparison of Fig. 38 with Fig. 37 shows the powerful development of the epidermis and prosenchyma composed here of strongly thickened cells possessing a small lumen. On the other hand, the parenchyma is reduced to two or at the most, near the vascular bundles, to three cell layers. The cells of the inner epidermis possess a small lumen and are compressed transversely.

The conditions found in *Lolium italicum* and *Festuca arundinacea* are typical of the other grasses.

Having described the nature of the tissue at the base of the lemma it will now be of interest to discuss the manner in which these tissues are affected by the penetrating coleorhiza of the germinating embryo. Under the pressure of the coleorhiza the thin-walled cells of the inner epidermis and the parenchyma are stripped off and frequently distorted. Next the coleorhiza strikes upon the prosenchymatous tissue. Under its pressure the cells of the prosenchyma are moved apart along the line of juncture of the long sclerenchymatous and the short cells of the base, there occurring no injury to the cells. As illustrated in Fig. 35 B this line runs along the oblique or transversal septae of the sclerenchymatous cells which remain completely intact. The spaces between the projecting ends of these cells were originally occupied by the short cells of the base of the lemma. Occasionally a few of these short basal cells adhere to the sclerenchymatous cells after the coleorhiza has broken through. (Fig. 35B, bb.)

The cells of the outer epidermis behave in a similar manner. Here the separation of tissues occurs along a line at which two series of cells differing as to form and physical characteristics meet, the thin-walled, almost transversely lying cells of the



lemma being separated from the strongly thickened, silicified cells of the base.

While these conditions are typical of *Lolium*, *Festuca*, *Arrhenatherum*, etc. it occasionally occurs with other grasses that the cells of the epidermis are rent by the coleorhiza.

The formation of the longitudinal slits is facilitated by the absence of the transverse processes of the walls and the lack of silicious cells at the base of the lemma. In yielding to the pressure of the coleorhiza in the longitudinal direction the cells of the epidermis and prosenchyma are pushed apart, the former remaining usually, the later as a rule, intact. (Fig. 34). These slits very often run along the fibrovascular bundles, where the thin-walled parenchyma occurs in several layers.

It should be added that the tracheal tissues are broken through transversely and separated from the base of the lemma.

#### ABNORMAL GERMINATION OF GRASS-FRUIITS.

Under normal conditions of germination the coleorhiza or the radicle appear first, and, as a rule, at the base of the lemma. At the beginning of this investigation several cases were observed of hulled grass-fruits developing first the coleoptile while nothing was to be seen at first of the radicle. A study of these cases brought out the fact that a majority of hulled grass-fruits show this type of germination which involves no physiological disturbance, but is the result of external factors, like mechanical resistance to and retardation of growth. The common feature of these abnormal cases is that the radicle does not break through at the base of the lemma. The different modes of abnormal germination have arbitrarily been arranged here in two groups.

Type A. The radicle appears either at the tip of the glumes or in the opening between the lemma and palet, below the tip of the lemma. The coleoptile appears, as a rule, outside the glumes sometime before the radicle emerges.

The following reasons account for the coleoptile appearing ahead of the radicle. The radicle growing first downwards, then bending at the base upwards covers in all cases a longer distance than the upwards growing coleoptile. In many cases the lemma is bent from the caryopsis thus exposing the coleoptile. Further, the caryopsis may be lifted by the pressure of the radicle; this

not only causes the coleoptile to appear first but also prolongs the distance covered by the radicle which first grows downwards to bend upwards on striking the base of the lemma. However, in several cases of abnormal germination the radicle was observed to appear ahead of the coleoptile (*Arrhenatherum*, *Alopecurus*, *Dactylis*, *Lolium*, *Poa*.)

Within Type A two forms of abnormal germination may be distinguished.

1. The lemma is bent from the caryopsis by a larger or lesser angle. The caryopsis is not raised in the glumes.

The majority of the abnormally germinating fruits show this type of germination. (*Lolium*, *Festuca*, *Poa*, *Cynosurus*, *Agrostis*). The angle at which the lemma is bent from the caryopsis varies generally from  $45^{\circ}$  to  $90^{\circ}$ . With *Setaria germanica* and *Phleum pratense* this angle may reach almost  $180^{\circ}$ . The radicle, emerging from the coleorhiza strikes upon the wall of the lemma, curves upwards and growing along the inner wall of the lemma appears at the tip of the latter.

2. The lemma adheres to the caryopsis or is slightly bent from it. The caryopsis, as a rule, is raised in the glumes.

*Alopecurus*, *Arrhenatherum*, *Holcus*, *Anthoxanthum*, *Avena*, etc. show this type of abnormal germination. The extending coleorhiza, on striking the base of the lemma, raises the caryopsis a short distance. The protruding radicle pushes first the caryopsis farther up, then bends upwards at a very sharp angle to appear at the apex of the glumes.

*Anthoxanthum*, *Holcus* and *Alopecurus*, which are surrounded also by the sterile glumes may exhibit a type of abnormal germination illustrated in Fig. 40. The radicle breaks through normally at the base of the lemma (Fig. 40B) and striking upon the base of the sterile glume turns upwards and appears between the tips of the sterile glumes.

Type B. The radicle does not appear at the apex of the glumes but directing its point against the base of the lemma it pushes the caryopsis out of the glumes and away for some distance. Figs. 39 and 44 illustrate this type of abnormal germination. With fruits enclosed also by the sterile glumes the radicle may push out the caryopsis alone (Fig. 39) or it may break through in the normal way at the base of the lemma and

TABLE 1.

## KIND OF GERMINATION

Kind of Grass	Normal	Expressed in Percentage of Total Germinated Grass-Fruits							Frequency of all kinds of abnormal germination
		Radicle appears at apex of fertile glumes	Radicle appears between tips of fertile or sterile glumes	Lemma and sterile glumes intact	Base of lemma broken through sterile glume intact	Caryopsis pushed away from fertile glumes; apex of radicle at base of lemma	Caryopsis with fertile glumes pushed out of sterile glumes; apex of radicle at base of sterile glumes	Radicle stunted or dead within fertile or sterile glumes	
<i>Alopecurus pratensis</i> (Meadow Foxtail)	50.3			15.6		14.9		19.1	30.5
<i>Alopecurus agrestis</i>	86.0			11.0				3.0	11.0
<i>Alopecurus geniculatus</i> (Flooding Foxtail)	54.2			7.0	2.2	16.2		20.4	25.3
<i>Anthoxanthum odoratum</i> (Sweet vernal-grass)	52.0			22.5	4.0	7.3	11.8	1.7	45.6
<i>Arrhenatherum elatius</i> (Oat grass)	25.0 82.7		11.0			63.5 1.2		0.5 4.1	74.5 13.1
<i>Avena pubescens</i>		11.9				2.3		1.4	14.6
<i>Cynosurus cristatus</i> (Crested Dogtail)	84.0	12.3				6.9		2.5	26.7
<i>Dactylis glomerata</i> (Orchard grass)	70.7	19.8							
<i>Festuca arundinacea</i> (Reed Fescue)									
<i>Festuca ovina</i> (Sheep's Fescue)	79.5	13.5	3.8						17.3
<i>Festuca pratensis</i> (Meadow Fescue)	55.2	6.6	22.5						29.2



TABLE 1—Concluded.

KIND OF GERMINATION				Expressed in Percentage of Total Germinated Grass-Fruits					Frequency of all kinds of abnormal germination
Kind of Grass	Normal	Radicle appears at apex of fertile glumes		Radicle appears between tips of fertile or sterile glumes		Caryopsis pushed away from fertile glumes; apex of radicle at base of lemma	Caryopsis with fertile glumes pushed out of sterile glumes; apex of radicle at base of sterile glumes	Radicle stunted or dead within fertile or sterile glumes	
		Lemma bent off	Lemma adhering to caryopsis	Lemma and sterile glumes intact	Base of lemma broken through sterile glume intact				
<i>Holcus lanatus</i> (Velvet grass)	85.0	13.0		18.3	21.7	6.6	28.3	13.0	
<i>Lolium italicum</i> (Italian Rye grass)	25.0		1.8					46.6	
<i>Lolium perenne</i> (Perennial Rye grass)	95.3	1.2						3.0	
<i>Phalaris arundinacea</i> (Reed Canary grass)	85.3	14.2						14.2	
<i>Phalaris canariensis</i> (Canary grass)	90.7	5.3				1.3	2.6	6.6	
<i>Poa compressa</i> (Canada Blue grass)	93.1	2.3				2.9	1.7	5.2	
<i>Poa nemoralis</i> (Wood Meadow grass)	27.7	61.0				4.5	6.8	65.5	
<i>Poa pratensis</i> (Kentucky Blue grass)	3.7	87.5				1.0	7.8	88.5	
<i>Poa trivialis</i> (Rough-stalked Meadow grass)	46.6	39.7					13.5	39.7	
	63.2	32.7					4.0	32.7	

move away the caryopsis, enclosed in the lemma and palet, from the sterile glumes.

Associated with the abnormal germination is a marked tendency to develop adventitious rootlets which spring from the hypocotyl or mesocotyl. This tendency is a result of the retardation in the growth of the primary radicle and reaches its highest degree in cases where the primary radicle becomes stunted and dies off. The frequently observed stunting and dying off of the radicle was found to be due to abnormal germination rather than to deficient viability.

In Table 1 is given the frequency occurrence of the normal and abnormal germination of fruits of twenty grasses. From this table the high percentage of abnormal germination in *Arrhenatherum*, *Poa nemoralis* and *Poa compressa*, *Holcus lanatus* will be noted. This table also shows a varying percentage of stunted or dead radicles, being highest with grass fruits which in addition to the fertile glume are surrounded, at germination, also by the sterile glumes.

In view of the high percentage of abnormal germination it became a matter of practical importance to determine whether this phenomenon occurs under natural conditions of germination in the soil. With this end in view a series of germination experiments were carried out with fruits of 9 grasses sown in pots filled with soil, the results of which are given in Table 2.

TABLE 2.

Kind of Grass	Number of fruits sown	Normal Germination	Abnormal Germination	Radicle died off within glumes
		Per cent of Germinated Fruits		
<i>Alopecurus pratensis</i>	400	98.0		1.7
<i>Arrhenatherum elatius</i>	100	100.0		
<i>Cynosurus cristatus</i>	100	100.0		
<i>Dactylis glomerata</i>	100	100.0		
<i>Festuca arundinacea</i>	400	99.0	0.3	0.6
<i>Festuca ovina</i>	100	100.0		
<i>Holcus lanatus</i>	200	90.0	6.0	3.0
<i>Lolium italicum</i>	200	100.0		
<i>Lolium perenne</i>	200	96.8	3.2	

The results presented in Table 2 show that under natural conditions prevailing in the soil abnormal germination either does not occur at all or only with a few grasses to a very slight

extent. On comparing Table 2 with Table 1 it will be seen that the stunting and dying off of the radicle within the glume is likewise occasioned by the artificial conditions prevailing in the germinator, and hardly occurs in the soil.

Before discussing briefly the causes of abnormal germination attention should be called to the fact that if a growing organism is to effect a certain performance it is essential that it be sufficiently anchored to prevent its being pushed back or bent aside. If this is not the case the organ will grow in the direction of least resistance.

Another point to be emphasized is that normally it is the coleorhiza that breaks through the tissues of the lemma. If the coleorhiza fails in this important function the conditions for abnormal germination are fulfilled.

Considering the most frequently occurring form of abnormal germination, where the lemma is bent from the caryopsis, it is obvious that here the pressure of the extending coleorhiza does not reach the intensity required to break through the base of the lemma. It does, however, reach an intensity sufficient to bend the lemma away from the caryopsis. The coleorhiza thus effects a performance in the direction of lesser resistance and the radicle, after escaping from the coleorhiza, is unable to penetrate the lemma and grows along the inner surface of the latter.

The same mechanical cause, though attended by a different external effect, brings about the other irregularities of abnormal germination. In those cases where the caryopsis is raised in the glumes the effort of the extending coleorhiza to break through the lemma is annulled by the caryopsis receding under pressure from the base of the lemma. The radicle upon leaving the coleorhiza may in turn raise the caryopsis somewhat and then bend upwards and appear at the tip of the glumes, or it may remain with its apex at the base of the glumes and push the caryopsis out and away sometimes for several centimeters from the glumes.

The degree of adhesion of the glumes to the caryopsis determines the kind of abnormal germination and is in turn influenced by the amount of moisture available in the germinator.

A quite distinct form of abnormal germination is shown by *Oryza sativa*. In a majority of examined seedlings it was found that the first signs of growth at germination are shown by the



coleoptile. Under the pressure of the epiblast the median vein or fibrovascular bundle yields, and in the narrow elliptical opening appear the coleoptile and the tip of the epiblast. This aperture extends downward, and the coleoptile shows several millimeters outside the glumes when the coleorhiza appears. Thus with *Oryza sativa* the coleorhiza and the coleoptile escape through the same opening.

### III. THE MECHANICAL AND BIOLOGICAL FUNCTION OF THE COLEORHIZA.

A brief description of the structure of the coleorhiza may serve to understand its functions.

The coleorhiza has the shape of a truncate cone. Its tissues consist of a mass of uniform cells covered by an epidermis extending to the apex of the coleorhiza. The form of the cells varies according to the stage of elongation of the coleorhiza. After the coleorhiza breaks through the glumes its cells appear in the middle section longitudinally extended, utricular, becoming shorter in the proximity of the apex terminating by thickened cells of the apical appendage. (Figs. 41 and 42).

The function of the coleorhiza is primarily mechanical in that it breaks the way for the radicle. It acts also as a protecting organ for the radicle. Nor is its function over with the penetration through the tissues of the glume. Soon after the coleorhiza breaks through the glume it sends out numerous trichomes or hairs whose length depends upon the grass species and the stage of gemination. These trichomes attain their greatest length at time when the radicle comes in contact with the soil or other substratum.

The trichomes act as fastening organs clinging to the particles of soil or other substratum, thus anchoring the germinating fruit.

In this investigation trichomes were observed on the coleorhiza of the following grasses: *Alopecurus pratensis*, *Alopecurus geniculatus*, *Alopecurus agrestis*, *Arrhenatherum elatius*, *Anthoxanthum odoratum*, *Anthoxanthum Puelii*, *Avena pubescens*, *Bromus Schraderi*, *Bromus arvensis*, *Brachypodium sylvaticum*, *Cynosurus*, *Dactylis glomerata*, *Elymus arenarius*, *Festuca pratensis*, *Festuca ovina*, *Festuca arundinacea*, *Festuca heterophylla*,

*Festuca rubra*, *Holcus lanatus*, *Koeleria cristata*, *Lolium italicum*, *Lolium perenne*, *Oryza sativa*, *Poa pratensis*, *Poa trivialis*, *Poa compressa*, *Setaria germanica* and *Phalaris arundinacea*.

After the coleorhiza has fulfilled its functions it is in turn broken through by the radicle. The radicle escapes from the coleorhiza through a lateral opening below the apex of the coleorhiza. Under the pressure of the radicle the cells of the coleorhiza become detached and are pushed apart without being injured.

#### POLYEMBRYONY IN GRASSES.

In the course of the present investigation the writer observed polyembryony in *Arrhenatherum elatius*, *Poa pratensis*, *Poa nemoralis*, and *Poa compressa*.

Diembryony occurred most frequently in *Poa pratensis*, (Fig. 43) with only two cases of fruits developing three embryos. Two cases of diembryony have been observed in *Poa nemoralis* and one case in *Poa compressa*.

A particularly fine case of diembryony has been observed in *Arrhenatherum elatius*. (See Fig. 44.) The individual seedlings were equally well developed and were united at the base of the hypocotyl possessing separate normal organs. As will be seen from Fig. 44 the emergence of the seedlings out of the glumes occurred in an abnormal manner, but their subsequent development was normal. It may be stated in this connection that in practically all cases of polyembryony the radicles emerged abnormally from the glumes.

#### ABNORMAL GERMINATION AS A POSSIBLE SOURCE OF ERRORS IN RECORDING RESULTS OF GERMINATION TESTS.

From a practical point of view some of the results of this investigation may have some significance in connection with the determination of the viability of grass seeds as determined by the germination test. The seeds of certain grasses are rather exacting as to conditions of germination, and the question of the influence of temperature, light and other physiological factors upon the germination of grass seeds still constitutes an important problem for research. It is then obviously important,

in the interest of greater accuracy and uniformity in recording results of germination tests, to determine the possible influence of any deviation in the germination from the normal upon the practical valuation of the viability of seeds as established by the germination test.

Two kinds of abnormality occur at germination of grass seeds on top of blotters: (a) the abnormal emergence of the radicle, and (b) the stunting and dying off of the radicle within the glumes. Relative to the first abnormality the germination test is usually carried for a sufficient length of time to allow the abnormally emerging radicle to appear at the tip of the glumes, and thus to become visible to the eye of the examiner. Such seeds should be considered as viable and otherwise normal since upon placing them in the soil they will grow normally.

The stunting and dying off of the radicle within the glumes, presents a more serious possibility of making errors in recording results of germination tests. Reference to Table 1 reveals that some of the grass seeds examined showed a rather high percentage of mortality of their radicle ranging from 0.5% for the Tall Oat grass to 28.3% for the Velvet grass. Now, the Rules for Seed Testing as adopted by the Association of Official Seed Analysts of North America at their meeting held in 1917 at Detroit, provide that "seeds of Gramineae should not be considered as germinated *unless both root and plumule elongate.*" On the strength of this rule all the seeds referred to above having developed a normal plumule but with no sign of a rootlet which is dead within the glumes, would be regarded as not germinated, which in certain cases would very appreciable misrepresent the actual degree of viability.

From Table 1 it will be seen that certain valuable grasses showed a percentage of mortality of their seed-rootlets a good deal higher than the margin of tolerance allowed in the seed laws. It would be advisable to check up the results of germination tests of such grasses as Velvet grass, Meadow Foxtail, Kentucky blue-grass and others, carried out on blotters, by subjecting the seed to a test in the soil. This would be especially advisable in cases where an appreciable number of seeds germinating in a chamber on blotters show the plumule but fail to develop the rootlet.



## LIST OF ILLUSTRATIONS.

Figure 33. *Lolium italicum*. Surface view of the epidermal cells in the middle section of the lemma. K, K<sub>1</sub>, silicious cells; iK, isolated silicious cell.

Figure 34. *Lolium italicum*. Basal part of the lemma showing epidermal cells in the region where the coleorhiza broke through. Note the initiation of a longitudinal slit along cell i.

Figure 35. *Lolium italicum*. A, a layer of sclerenchymatous cells in the middle section of the lemma; B, sclerenchymatous cells at the base of the lemma where the coleorhiza broke through; C, single sclerenchymatous cell; b, b<sub>1</sub>, short cells severed from the base of the lemma.

Figure 36. *Festuca arundinacea*. Part of transverse section through the base of the lemma, below the region where the coleorhiza breaks through; ae, outer epidermis; h, prosenchyma; p, parenchyma.

Figure 37. *Festuca arundinacea*. Part of transverse section through the lemma in the region where the coleorhiza breaks through. ae, outer epidermis; h, prosenchyma; p, parenchyma; ie, inner epidermis; g, lateral fibrovascular bundle.

Figure 38. *Festuca arundinacea*. Transversal section through the lemma above the line of rupture, representing the part between the lateral and marginal fibrovascular bundles. ae, outer epidermis; ps, prosenchyma; p, parenchyma; ie, inner epidermis; K, silicious cell.

Figure 39. *Alopecurus pratensis*. Abnormal germination: The radicle pushed the germinating caryopsis out of the sterile and fertile glumes. K, caryopsis; r, radicle; col., coleorhiza; c, coleoptile; pb, plumule; K<sub>1</sub>, sterile glumes.

Figure 40. *Holcus lanatus*. Abnormal germination: A, the caryopsis is raised in the sterile glumes with the radicle appearing at their tip. B, the germinating caryopsis, K, after removal of sterile glumes. After normally breaking through the lemma, the radicle, r, grew upward along the sterile glume; c, coleoptile; dk, lemma; vs, palet.

Figure 41. *Hordeum sativum*. Longitudinal section through apical part of the coleorhiza. The upper delicate elliptical cells become thicker toward the apex and terminate by thick-walled cells of the apical appendage.

Figure 42. *Festuca arundinacea*. Surface view of the expanded apical appendage.

Figure 43. Polyembryony in *Poa pratensis*. K, caryopsis; r, r<sub>1</sub>, abnormally extending radicles; c, c<sub>1</sub>, coleoptiles; p, p<sub>1</sub>, plumules; ds, lemma; vs, palet.

Figure 44. Polyembryony in *Arrhenatherum elatius*. K, caryopsis; r, r<sub>1</sub>, radicles pushing the seedling out of the glumes; c, c<sub>1</sub>, the two equally favored coleoptiles; col, col<sub>1</sub>, coleorhizas; sp, fertile glumes.

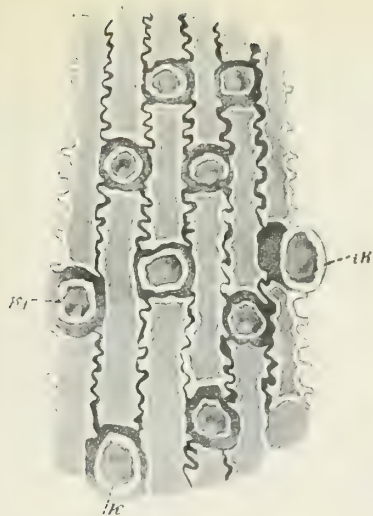


FIG. 33.

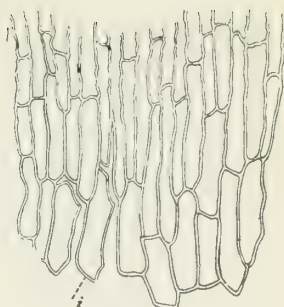


FIG. 34.



FIG. 35.



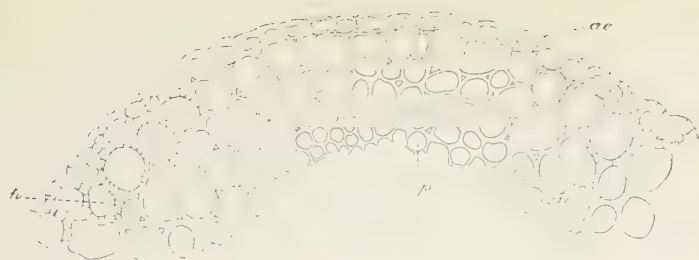


FIG. 36.



FIG. 37.



FIG. 38.





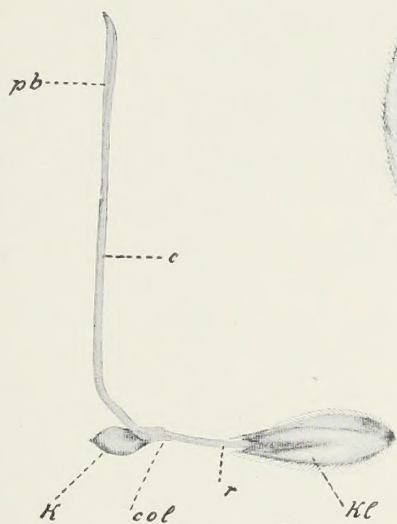
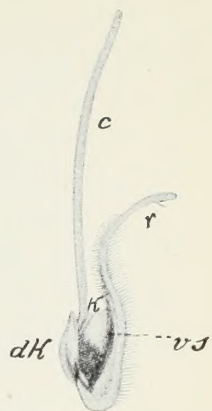


FIG. 39.



A



B

FIG. 40.

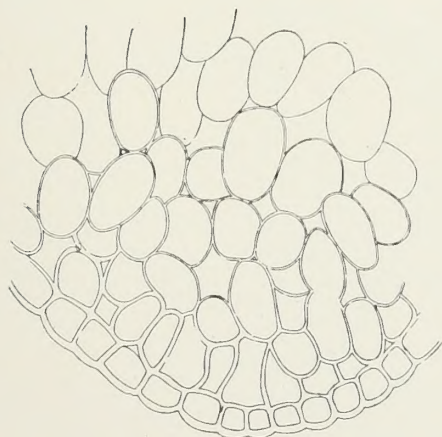


FIG. 41.

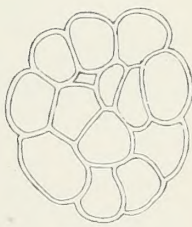


FIG. 42.



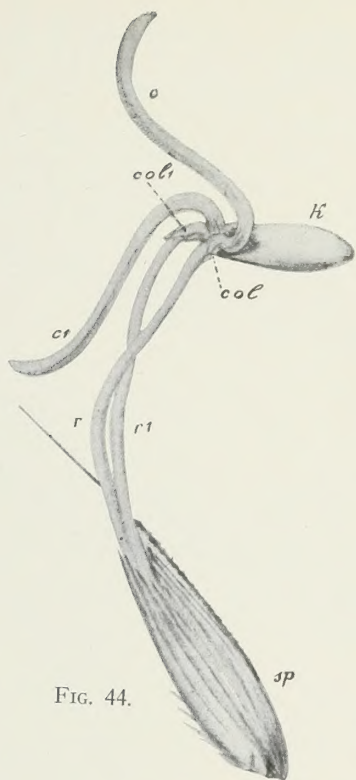


FIG. 44.

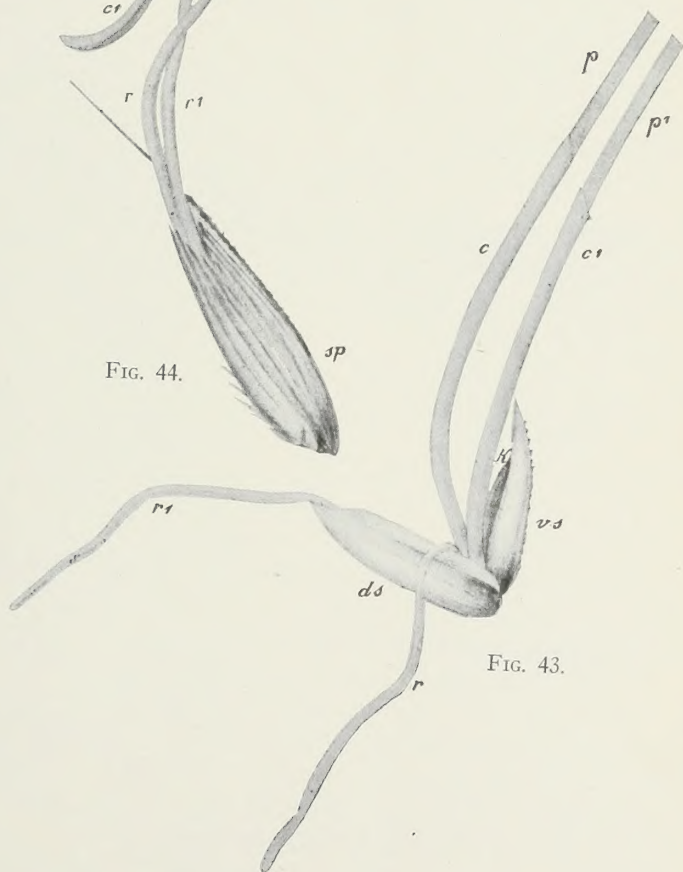


FIG. 43.



